

Growth Changes in Measurements of Upper Facial Positioning

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ABSTRACT Growth changes in the position of the midline upper face are examined for samples of *Pan troglodytes*, *Gorilla gorilla*, and modern humans. Horizontal and vertical distances between nasion and the anterior end of the cribriform plate are plotted against stage of dental development. Kendall's nonparametric correlations between facial positioning and stage of dental development are tested for significance.

In African apes, the upper face becomes more projecting and positioned higher relative to the anterior cranial base. The extent of this horizontal and vertical separation reflects primarily facial size. In modern humans, the upper face becomes more projecting but is relatively stable in its vertical position. Comparison of *Pan* and modern human crania in the youngest dental age category indicates that the upper face of modern humans is positioned lower early in postnatal life.

The position of the upper face (glabella) relative to the anterior and posterior cranial base is presented for several fossil hominid crania. The fossil crania are similar to *Pan* and modern humans in facial projection relative to the anterior cranial base. However, glabella is positioned low in the fossil crania. Total facial projection (relative to nasion) for Sts 5 is similar to the mean for *Gorilla*. Fossil *Homo* and robust australopithecine crania display very projecting upper faces. We suggest that the upper face of *Homo* is projecting due to the length of the anterior cranial fossa, while robust australopithecines possess a thick frontal bone. *Am J Phys Anthropol* 108:269–280, 1999.

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The craniofacial relationship is a critical feature of the mammalian skull since it involves juxtaposition of cranial components with distinct functional roles and developmental histories (Kohn, 1991). The position of the upper face relative to the neurocranium varies considerably among early hominid crania, and recent ontogenetic studies have provided a useful perspective for the analysis of taxonomic variation in facial positioning (Bromage, 1992; McCollum, 1997).

Previous studies have focused on separate aspects of facial positioning. The vertical position of the upper face is often referred to as facial hafting (McCollum, 1994), while

the horizontal separation between the face and neurocranium is termed facial projection. Most measurements of facial positioning have been made relative to external neurocranial landmarks (Bilsborough and Wood, 1988; Schultz, 1955; Tobias, 1967). A problem encountered when using external landmarks is that measurements of facial positioning may be influenced by variation in the size and shape of the brain.

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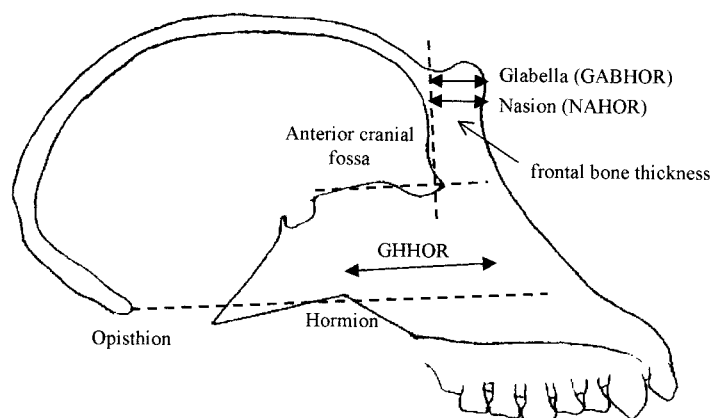


Fig. 1. Measurements of upper facial projection. NAHOR and GABHOR are horizontal distances between the upper face and the anterior base point. These distances are measured along a line defined by tuberculum sella and the anterior base point. GHOR is the horizontal distance between the upper face and hormion taken along the opisthion-hormion line.

In this study, distances between landmarks of the midline upper face and anterior cranial base are used to characterize the craniofacial relationship. Basic growth changes in these dimensions remain poorly documented for extant hominoids. An advantage of our measurements is that they reflect the craniofacial relationship without including brain size as part of the measurement.

We document and discuss growth changes in upper facial positioning for *Pan troglodytes*, *Gorilla gorilla*, and modern humans. The main objective of this study is to describe growth changes in upper facial positioning relative to the internal cranial base. Growth changes are assessed using the stage of dental development as a baseline. Of particular interest is the development of species differences in upper facial positioning. The three extant species should be similar in the youngest dental age category if differences in facial positioning are entirely postnatal in origin. We also present facial positioning measurements for fossil hominid crania and interpret species differences as they relate to the results of the growth study.

MATERIALS AND METHODS

The sample consists of postnatal growth series of *Pan troglodytes*, *Gorilla gorilla*, and modern human crania which are part of the Hamann-Todd collection housed at the Cleveland Museum of Natural History. Additional juvenile human crania housed at the Armed Forces Institute of Pathology are also included. For this analysis, each cranium is assigned a score (DENTAGE) which indi-

cates the number of permanent maxillary molars in occlusion. DENTAGE is coded as follows: 0, deciduous molars; 1, first permanent molars; 2, second permanent molars; 3, third permanent molars. The stage of dental development is a useful baseline for examination of growth changes (Ashton, 1957; Laitman et al., 1978), and our classification system provided sufficient discrimination among crania to detect growth changes.

Measurements of the position of nasion relative to the anterior cranial base are shown in Figures 1 and 2. On tracings from lateral radiographs, a perpendicular from nasion is projected onto a line defined by tuberculum sella and the anterior end of the cribriform plate (at the intersection with the internal contour of the frontal bone). The latter point is designated the anterior base point (abp). Vertical (NAVERT) and horizontal (NAHOR) distances between nasion and the anterior base point were measured using Mitutoyo digimatic calipers. Radiographic measurements are corrected for enlargement using the distance between the median plane of the cranium and the radiographic film. The correction was found to be quite accurate; mean differences between corrected radiographic measurements and corresponding caliper measurements are less than 1 mm. As illustrated in Figure 1, projection of nasion beyond the anterior end of the cribriform plate (NAHOR) reflects in large part the thickness of the frontal bone. The vertical separation between these points (NAVERT) (Fig. 2) may be primarily a reflection of total facial height (see below).

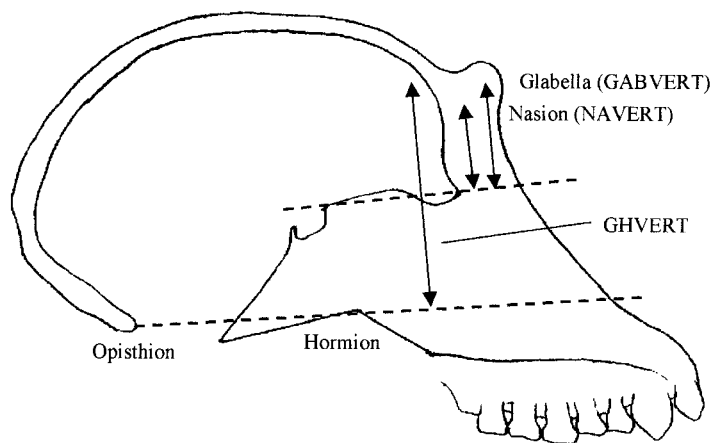


Fig. 2. Measurements of vertical facial positioning. NAVERT and GABVERT are vertical distances between the upper face and the anterior base point. GHVERT is the vertical distance between the upper face and hormion.

The two measurements of facial positioning are plotted against DENTAGE. Correlations between facial positioning measurements and DENTAGE are calculated for each species. Since one of the variables is only ordinal in scale, a nonparametric correlation coefficient (Kendall's tau) is tested for significance. Correlations are tested for total and single-sex samples.

Facial positioning measurements were collected for several early hominid crania. Since the front-nasal suture at nasion is frequently obliterated in adult crania, glabella was used instead to indicate the midline position of the upper face. Glabella is not intended as a surrogate landmark for nasion since the relationship between nasion and glabella is not constant. To describe the relationship between nasion and glabella, we calculated vertical and horizontal distances between these landmarks (relative to the anterior cranial base line) for adult samples of our three species. For every individual in each species, glabella is positioned superior and anterior to nasion. The vertical separation between these landmarks is greater than the horizontal. Thus, there is at least a consistent relationship between glabella and nasion in our extant groups, and we suggest that the results of our growth study may be used to interpret variation in upper facial positioning using glabella.¹

¹For adult *Pan*, the mean vertical distance between glabella and nasion is 9.3 mm ($S = 2.8$, $n = 21$), and the mean horizontal distance is 3.0 mm ($S = 1.4$). Distances for adult *Gorilla* were similar to those for *Pan*. In modern humans, the mean vertical distance is 12.4 mm ($S = 3.1$, $n = 38$), and the mean horizontal distance is 4.3 mm. ($S = 1.5$).

The horizontal (GABHOR) and vertical (GABVERT) position of glabella relative to the anterior cranial base was calculated using coordinate data for original specimens attributed to *Australopithecus africanus* (Sts 5, housed at the Transvaal Museum) and for *A. aethiopicus* (KNM WT 17000, housed at the Kenya National Museum). These measurements were also calculated for a digitized cast of a specimen attributed to archaic *Homo sapiens* (Arago). These measurements were calculated trigonometrically from coordinate data using an angle (tuberculum sella–anterior base point–glabella) and a distance (anterior base point–glabella).

Since internal landmarks are often inaccessible in fossil crania, the position of glabella was also assessed relative to the posterior cranial base. These measurements were derived from coordinate data collected from original fossil crania. Vertical (GHVERT) and horizontal (GHHOR) distances between glabella and hormion were derived from coordinate data collected for each skull (Figs. 1, 2). Using an angle (nasion–hormion–opisthion) and a distance (nasion–hormion), a perpendicular from nasion is projected to the opisthion–hormion line and distances calculated trigonometrically. Measurements relative to hormion were calculated for fossil crania attributed to *A. africanus* (Sts 5), *A. boisei* (KNM ER 406), and *Homo erectus* (KNM ER 3733). Coordinates were also collected from a cast of a specimen attributed to archaic *Homo sapiens* (Kabwe). These measurements are compared to adult means for

TABLE 1. Mean and standard error of the mean for (NAHOR) and (NAVERT) in *Pan*¹

DENTAGE		NAHOR		NAVERT	
		Mean	SEM	Mean	SEM
0	(U)	10.7 (5)	0.3	7.2	1.2
1	(T)	14.6 (12)	0.9	8.4	1.2
	(M)	12.2 (1)	—	5.1	—
	(F)	16.9 (5)	1.2	11.2	0.9
2	(U)	13.0 (6)	1.1	6.7	1.9
	(T)	17.5 (14)	0.6	10.7	1.1
	(M)	18.3 (4)	1.8	10.1	2.7
	(F)	17.2 (7)	0.5	11.2	1.5
3	(U)	17.1 (3)	0.8	10.4	2.1
	(T)	22.4 (22)	0.7	14.2	0.7
	(M)	23.8 (11)	1.1	14.5	1.0
	(F)	20.9 (11)	0.6	14.0	0.9

¹ All measurements are in millimeters. Sample sizes are in parentheses next to the mean values. NAHOR, horizontal distance between nasion and the anterior base point; NAVERT, vertical distance between nasion and the anterior base point; T, total sample; M, males; F, females; U, sex unknown.

TABLE 2. Correlations between measurements of facial positioning and DENTAGE¹

	NAHOR	NAVERT
<i>Pan</i>		
T	.72** (53)	.49**
M	.56** (16)	.44*
F	.61** (23)	.33*
<i>Gorilla</i>		
T	.75** (44)	.37**
M	.81** (18)	.58**
F	.67** (21)	.27
Modern humans		
T	.55** (61)	.27**
M	.30* (39)	.29*
F	.67** (18)	.24

¹ Sample sizes for each correlation are in parentheses next to means for NAHOR. DENTAGE, score that indicates the number of permanent maxillary molars in occlusion; NAHOR, vertical distance between nasion and the anterior base point; T, total sample; M, males only; F, females only.

* $P < .05$.

** $P < .01$.

African apes and modern humans, and species differences are discussed in relation to the growth study.

RESULTS

Table 1 lists summary statistics for NAHOR and NAVERT by DENTAGE and sex for *Pan*. Table 2 lists Kendall's tau coefficients for correlations between facial positioning measurements and DENTAGE for all three species. In *Pan*, upper facial projection increases from the dm to M3 stage in the total and single-sex samples (Fig. 3a). Males ultimately attain a more projecting face than females. NAVERT increases from dm to M3 stage (Tables 1, 2).

While the *t*-test for sex differences in adults indicated that males have a face positioned higher relative to the cribriform plate, the difference is not as large as for facial projection. In the youngest age category, *Pan* and modern humans are not significantly different in the degree of upper facial projection.

Table 3 presents summary statistics for facial positioning measurements in *Gorilla*. Facial projection increases significantly for total and single-sex samples. Males attain a more projecting upper face than females, and divergence between males and females seems to occur after the M2 stage (Table 3; Fig. 3b). NAVERT also increases in total and males-only samples (Table 3; Fig. 4b). We did not detect a significant increase in NAVERT for female gorillas. This is probably due to small sample size for this subgroup since total facial height does increase in female gorillas during postnatal growth (Moore and Lavelle, 1974). The upper face of adult males is positioned higher than that of females. At the M1 stage, nasion in *Gorilla* is higher relative to the anterior base segment than in *Pan* at the same stage.

Table 4 lists summary statistics for facial positioning measurements in modern humans. Upper facial projection increases in modern humans in the total and single-sex samples. The greatest increase occurs between the dm and M1 stage (Table 4; Fig. 3c). NAVERT increases slightly in the total and males-only samples. The *t*-test indicates that the upper face of modern humans is positioned lower than that of *Pan* in the youngest dental age category.

Variation among fossil hominid crania

Table 5 lists measurements of upper facial positioning (relative to both cranial base points) for selected fossil hominid crania. Figure 5 plots measurements of facial positioning relative to the anterior base point for African apes, modern humans, and fossil hominids. The fossil crania are quite uniform in the degree of facial projection and are most similar to *Pan* and modern human males (Fig. 5a). The upper face of the fossil crania is positioned lower than that of African apes, and all three fossil crania are at the low end of the modern human range for this measurement (Fig. 5b).

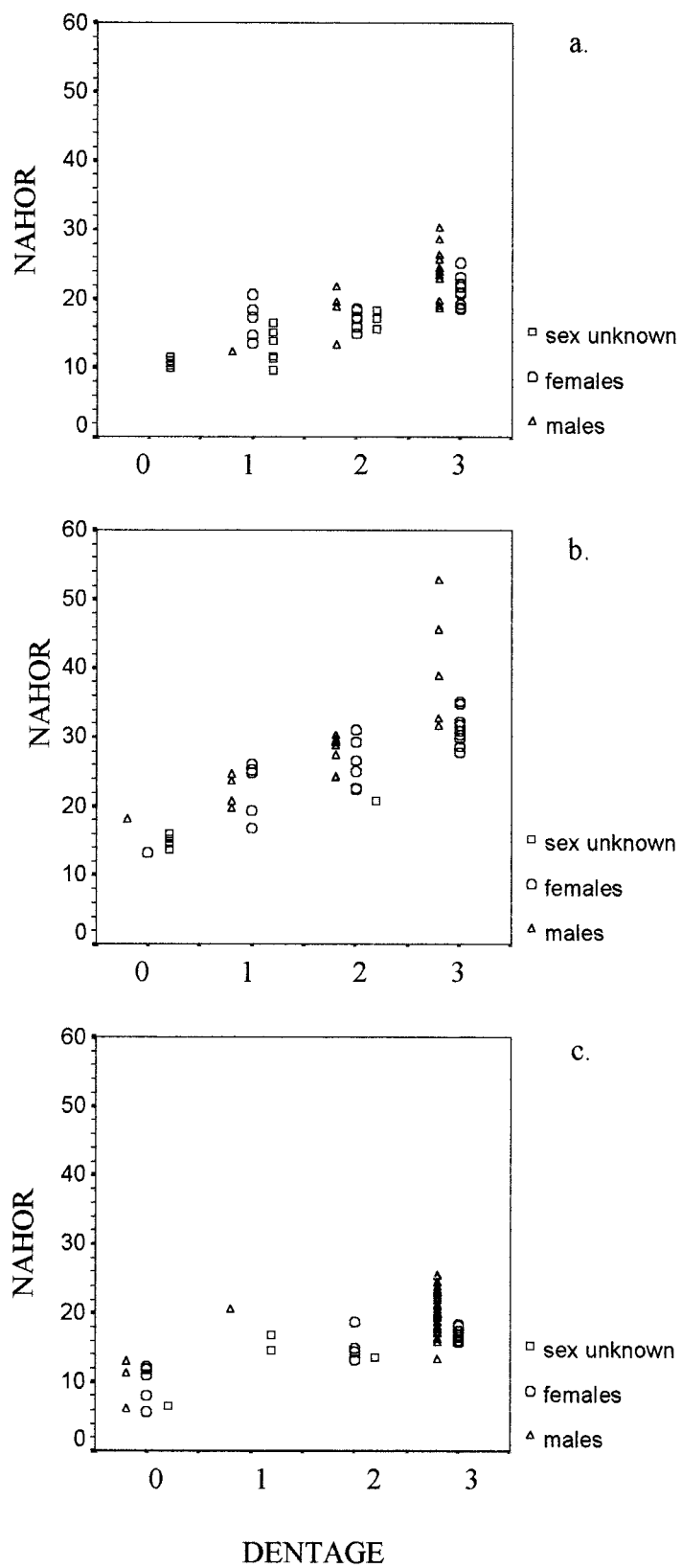


Fig. 3. NAHOR plotted against DENTAGE for *Pan* (a), *Gorilla* (b) and modern humans (c).

TABLE 3. Mean and standard error of the mean for NAHOR and NAVERT in *Gorilla*¹

DENTAGE		NAHOR		NAVERT	
		Mean	SEM	Mean	SEM
0	(T)	15.2 (6)	0.8	13.8	1.8
	(M)	18.1 (1)	—	15.1	—
	(F)	13.2 (1)	—	10.8	—
	(U)	14.9 (4)	0.5	14.3	2.6
1	(T)	22.2 (9)	1.1	18.1	1.4
	(M)	22.0 (4)	1.2	18.6	1.6
	(F)	22.4 (5)	1.8	17.8	2.3
2	(T)	26.7 (15)	0.8	23.1	1.6
	(M)	27.8 (8)	0.9	26.5	2.2
	(F)	26.2 (6)	1.4	18.9	1.4
	(U)	20.7 (1)	—	20.5	—
3	(T)	34.5 (14)	1.9	24.2	2.0
	(M)	40.2 (5)	4.0	31.2	2.6
	(F)	31.3 (9)	0.8	20.4	1.9

¹ All measurements are in millimeters. Sample sizes are in parentheses next to the mean values. F, females; M, males; NAHOR, vertical distance between nasion and the anterior base point; NAVERT, horizontal distance between nasion and the anterior base point; T, total sample; U, sex unknown.

Figure 6 compares horizontal and vertical distances between glabella and hormion. The upper face of Sts 5 is more projecting than that of *Pan* and is most similar to the mean for female *Gorilla* (Fig. 6a). The upper face of KNM ER 406 is closest to the mean for modern human males. The archaic *Homo sapiens* specimen (Kabwe) and KNM ER 3733 are at the upper end of the modern human range in terms of upper facial projection.

The upper faces of the two australopithecine crania (Sts 5 and KNM ER 406) are positioned lower than those of African apes but higher than in modern humans. In the two genus *Homo* crania (Kabwe and KNM ER 3733), the upper face is positioned slightly higher than that of modern humans.

DISCUSSION

The pattern of growth changes in the upper face relative to the cranial base in African apes has not been well documented in previous studies. The growth pattern of their middle and lower face is generally characterized as downward and forward (Krogman, 1931a,b). Krogman used superimposed tracings of growth series of apes to document the growth pattern of the cranium. However, the skulls were oriented along a nasion-porion registration line, thus obscuring changes in the position of the upper face relative to the cranial base.

In this study, upper facial projection was found to increase in African apes, with *Gorilla* ultimately attaining the most projecting upper face. By the eruption of the first permanent molar, the upper face of *Gorilla* is positioned much higher than that of *Pan*. Growth changes in these measurements of facial positioning in African apes are presumably secondary to a general increase in the dimensions of the upper face. Supero-inferior and antero-posterior expansion of the upper facial skeleton leads to horizontal separation between the inner and outer tables of the frontal bone and to vertical separation between nasion and the plane of the anterior cranial base (see below). Thus, we suggest that differences in upper facial positioning between *Pan* and *Gorilla* are largely the result of differences in facial size.

Previous experimental studies have documented a different growth pattern for sutural landmarks of the middle and lower face. In a longitudinal implant study, Sarnat (1976) found that these sutural landmarks moved anteriorly and inferiorly relative to the floor of the anterior cranial fossa.

Although sample sizes are small, this study reveals sex differences in the ontogeny of facial positioning in *Gorilla*. Sex differences in facial projection seem to arise after the M2 stage, while differences in the vertical position are already evident at the M2 stage. We detect little change in vertical facial positioning in female gorillas between the M1 and M3 stages.

Previous studies have attempted to explain underlying mechanisms of sexual dimorphism in anthropoids. Sirianni and Van Ness (1978) suggested that sex differences in adult macaque cranial base dimensions were the result of the increased rate and duration of growth in males. In a recent study (Leigh and Shea, 1996), adult body size dimorphism in *Gorilla* was found to result from a combination of sex differences in the rate and duration of somatic growth. Since systemic growth exerts a greater effect on facial dimensions than on other skull components (Ravosa, 1991), sex differences in facial positioning may be the result of similar ontogenetic mechanisms.

Leigh and Shea (1996) also concluded that, in *Gorilla*, male and female somatic

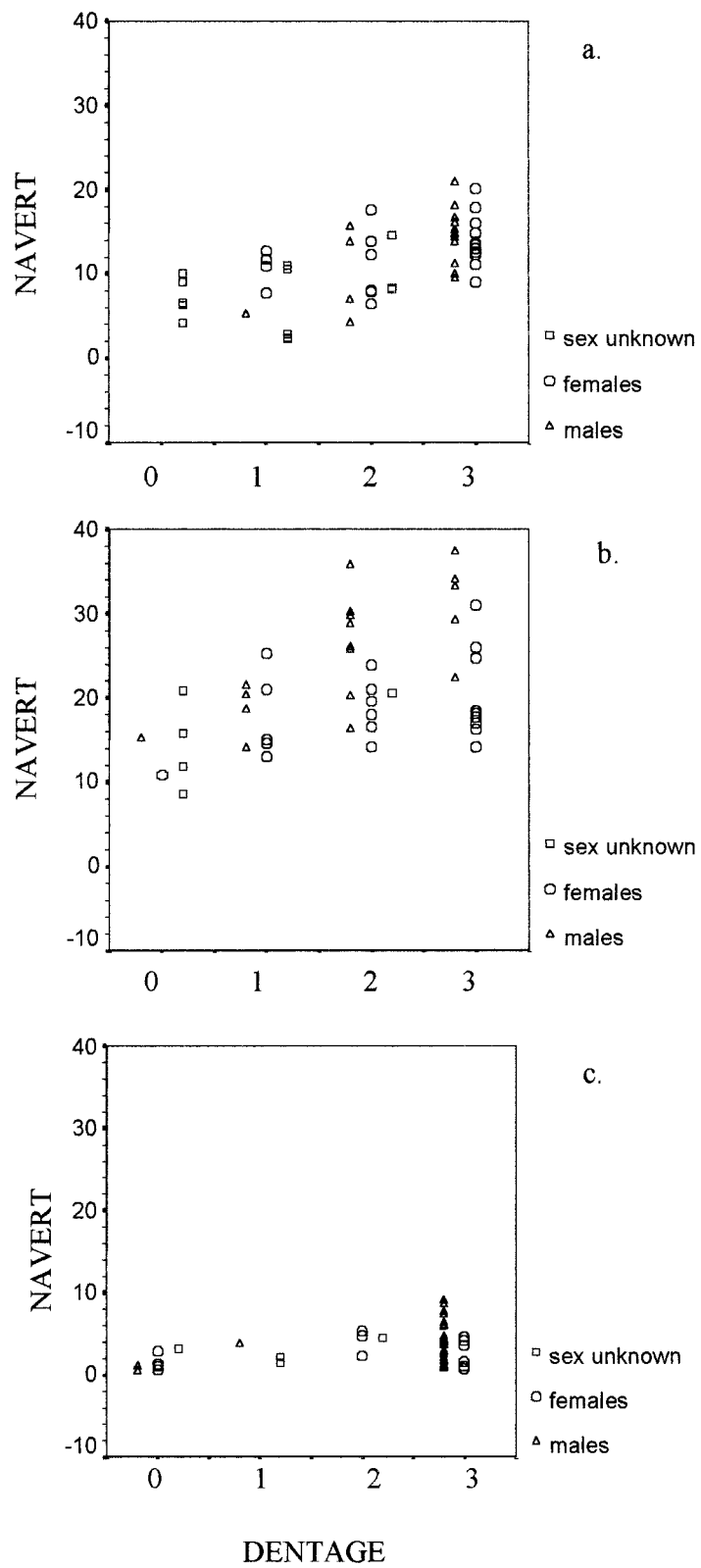


Fig. 4. NAVERT plotted against DENTAGE for *Pan* (a), *Gorilla* (b) and modern humans (c).

TABLE 4. Mean and standard error of the mean for NAHOR and NAVERT in modern humans¹

DENTAGE		NAHOR		NAVERT	
		Mean	SEM	Mean	SEM
0	(T)	9.5 (9)	1.0	1.4	0.3
	(M)	10.0 (3)	2.0	0.8	0.2
	(F)	9.8 (5)	1.3	1.3	0.4
	(U)	6.4 (1)	—	3.1	—
1	(T)	17.3 (3)	1.7	2.5	0.6
	(M)	20.5 (1)	—	3.7	—
	(U)	15.7 (2)	—	1.9	0.4
2	(T)	15.0 (5)	1.2	3.8	0.6
	(F)	15.3 (4)	1.0	3.6	0.8
	(U)	13.6 (1)	—	4.4	—
3	(T)	19.4 (44)	0.5	4.0	0.4
	(M)	20.1 (35)	0.5	4.1	0.5
	(F)	16.8 (9)	0.3	3.3	0.9

¹ All measurements are in millimeters. Sample sizes are in parentheses next to the mean values. F, females; M, males; NAHOR, vertical distance between nasion and the anterior base point; NAVERT, horizontal distance between nasion and the anterior base point; T, total sample; U, sex unknown.

TABLE 5. Measurements of upper facial positioning for fossil hominid crania¹

	GABHOR	GABVERT	GHHOR	GHVERT
KNM WT 17000	24.9	7.7	—	—
KNM ER 406	—	—	72.5	50.3
Sts 5	27.2	9.5	58.9	48.1
KNM ER 3733	—	—	79.2	28.8
Arago	26.3	9.8	—	—
Kabwe	—	—	85.8	28.6

¹ GABHOR and GABVERT are distances (in millimeters) between glabella and the anterior base point. GHHOR and GHVERT are distances between glabella and hornion.

growth trajectories diverge approximately between 6 and 7 postnatal years. The timing of ontogenetic divergence in general somatic growth trajectories is at least consistent with the divergence in our measurements of facial positioning. In the present study, sex differences in facial positioning were evident after the eruption of the first permanent molar, which is largely complete by 4 years of age (Aiello and Dean, 1990).

Growth changes in upper facial projection have been described for modern humans. Knott (1971) measured frontal bone thickness (nasion to posterior wall of frontal sinus) in a longitudinal sample of modern humans aged 5 to adult. Upper facial projection increased gradually in both sexes, and on average the increase was greater in males than in females. Scott (1958) documented an increase in the distance between nasion and

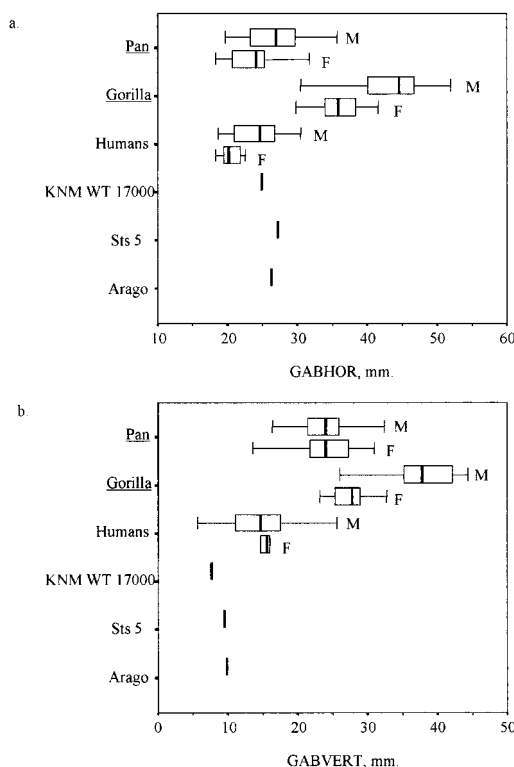


Fig. 5. Boxplots of GABHOR (a) and GABVERT (b) for African ape, modern human, and several fossil hominid crania. The vertical line in the box is the median, and the limits of the box represent the 50% range. The whiskers indicate the maximum and minimum values.

foramen cecum from birth to adulthood. Early, rapid increase in this dimension was followed by stability during early adolescence and then a regular increase to adulthood. This pattern of change is similar to the one documented in the present study. Although there appears to be no increase in the facial projection from the M1 to M2 stage (Fig. 3), four of the five M2 individuals are females. As sex differences in facial positioning are evident by this stage (Knott, 1971), overall increase in this dimension may be obscured.

The vertical position of the face has been found to be relatively stable in modern humans during postnatal development. Ford (1958) examined growth changes in the height of nasion above the cribriform plane in modern humans aged neonatal to adult. As in the present study, no regular increase

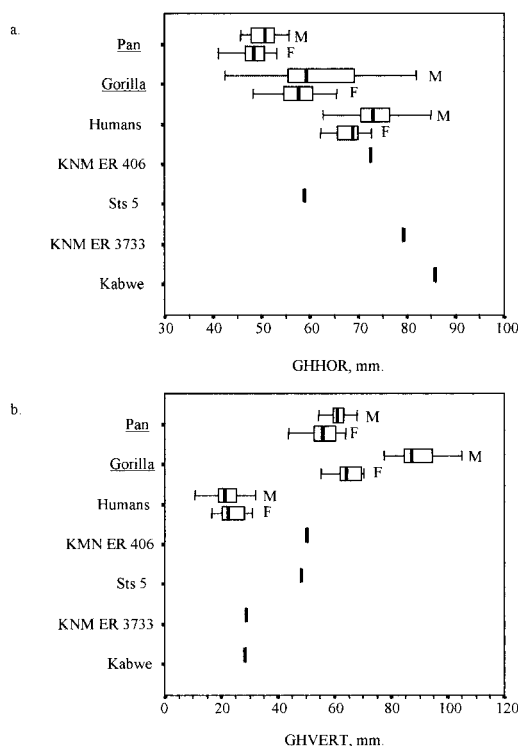


Fig. 6. Boxplots of GHHOR (a) and GHVERT (b) for African ape, modern human, and several fossil hominid crania.

in this dimension was found. Adult dimensions for his measurement are slightly higher than reported here, probably owing to the slight difference in the reference line.

The results of this study indicate that differences between African apes and modern humans in the vertical position of nasion are established during prenatal or early postnatal development. Compared to *Pan* crania in the deciduous molar category, modern human crania have an upper face positioned significantly lower relative to the anterior base segment. However, *Pan* and modern humans are initially quite similar in the projection of the upper face. These early differences in vertical facial position may relate to species differences in the pattern of early brain growth.

Possible mechanisms of change in facial positioning

Depending upon which cranial base reference point is used, measurements of upper

facial positioning may reflect growth progress of somatic and neural functional matrices contiguous with the cranial base and face. Measurements of facial projection relative to the anterior end of the cribriform plate reflect separation between inner and outer tables of the frontal bone. Cortical drift of the external table of the frontal bone leads to an increase in upper facial projection (Enlow, 1990). Growth of the facial aspect of the frontal bone is a compromise between the demands of functional matrices such as orbital contents, respiratory mucosa, and hematopoietic diploe within the bone (Moss and Young, 1960). Antero-posterior growth of the upper facial complex may also reflect growth of nasal, pharyngeal, and even oral matrices (Moss, 1962). The fact that experimental hydrocephaly in rats had minimal effect on the morphology of the upper facial skeleton (Moss and Young, 1960) suggests that separation between inner and outer tables of the frontal bone is not directly related to neural expansion.

Ontogenetic changes in the vertical position of nasion relative to the anterior base segment reflect compensatory growth at the frontonasal suture. Superior displacement of the upper face relative to the anterior cranial base in apes is possible given the spatial relationship between the face and the anterior pole of the brain. Superior growth of the upper face is prevented in modern humans by the presence of the overlying neural mass.

Gross spatial relationships between bones of the neurocranial and facial skeleton may be established during fetal life in humans (Moss et al., 1956). Minor adjustments of facial position (mostly projection) occur during postnatal development. The fact that, in the youngest age category, the upper face of modern humans is positioned lower than in *Pan* suggests that differences in facial positioning extend to the prenatal period. These differences in vertical facial positioning may relate to prenatal differences in the rate of cerebral expansion. Cerebral expansion in modern humans has been linked to repositioning of the upper facial skeleton (Biegert, 1963; Weidenreich, 1941).

Pan and modern human crania are similar in the measurement of frontal bone

thickness (GABHOR) (Fig. 5). However, when upper facial projection is assessed relative to hormion (GHHOR) (Fig. 6), modern humans have very projecting upper faces. This difference reflects species differences in the length of the anterior cranial fossa. Measurements of upper facial projection relative to points along the posterior cranial base (e.g., hormion) reflect both frontal bone thickness and the length of the anterior cranial fossa. The length of the anterior cranial fossa in turn is influenced in large part by the length of the frontal lobes of the brain. Thus, the relatively large frontal lobes of modern humans contribute greatly to the measurement of total facial projection.

In humans, growth at the fronto-ethmoidal suture until about 7 years of age facilitates expansion of the frontal lobes of the brain (Bjork, 1955; Scott, 1958). After this time, any increase in total facial projection (GHHOR) must be accomplished primarily by bone deposition at nasion. Given the relatively small frontal lobes of *Gorilla* compared to modern humans, upper facial projection in *Gorilla* is strongly influenced by the thickness of the frontal bone.

Variation among fossil hominid crania

Comparison of facial positioning relative to the anterior and posterior cranial base reveals an interesting pattern of interspecific variation. Although these dimensions are partly a function of cranial size, the pattern of variation suggests fundamental species differences in both aspects (vertical and horizontal) of the craniofacial relationship which are unrelated to cranial size. Relative to the anterior cranial base, australopithecine crania are similar to African apes in the degree of facial projection. However, measurements from hormion indicate that the upper face of Sts 5 is more projecting than that of *Pan* and that that of KNM ER 406 is similar to modern humans. Since the anterior component of facial projection (GABHOR) in Sts 5 is very similar to *Pan*, the greater degree of projection relative to hormion may reflect a long anterior cranial fossa.

It is unlikely that extreme facial projection in the *A. boisei* specimen is related to the length of the anterior cranial fossa. As

noted earlier, facial projection from hormion reflects both the length of the frontal lobes and the separation between the face and anterior cranial base. Since the frontal lobes of robust australopithecines seem to have been small (Holloway, 1988), extreme facial projection in KNM ER 406 probably indicates considerable separation between the upper face and the anterior terminus of the cranial base.

The crania attributed to *Homo erectus* (KNM ER 3733) and archaic *Homo sapiens* (Kabwe) are most similar to modern humans in upper facial positioning. These specimens have quite projecting upper faces relative to hormion. The anterior component of facial projection (GABHOR) could not be measured for these specimens. Thus, their extreme facial projection could reflect a long anterior cranial fossa and a thick frontal bone.

Relative to the anterior cranial base, the upper face of australopithecines and archaic *Homo sapiens* is positioned quite inferiorly. This measurement of facial positioning in Sts 5 is consistent with previous descriptions. Ashton and Zuckerman (1951) and Tobias (1967) found that, according to the supraorbital height index, Sts 5 was similar to modern humans in the vertical position of the upper face. The inferior position of the upper face in KNM WT 17000 is surprising, given the generally primitive nature of this specimen. However, specialized enlargement of the masticatory apparatus which characterizes this specimen might also alter the growth pattern of the upper face. Unfortunately, it was not possible to collect this measurement for later robust australopithecine crania.

Relative to hormion, the australopithecine upper face is positioned lower than that of *Gorilla* and *Pan* but higher than that of modern humans. Using a supraorbital height index developed by Le Gros Clark (1950), previous studies have found that the robust australopithecine face is hafted high relative to the top of the neurocranium (Ashton and Zuckerman, 1951; Tobias, 1967). Using a different measurement of facial positioning, McCollum (1994) also concluded that the *Paranthropus* upper face is positioned high relative to the cranial base. Measure-

ments of facial positioning relative to the anterior cranial base would improve our understanding of the craniofacial relationship in robust australopithecines.

The inferior position of the face in specimens attributed to archaic *Homo sapiens* is consistent with the large anterior cranial fossae in these specimens. Expansion of the frontal lobes of the brain may have altered the craniofacial relationship early in development, restricting superior growth of the face.

CONCLUSIONS

We have documented growth changes in the craniofacial relationship for *Pan*, *Gorilla*, and modern humans. Measurement of upper facial positioning relative to the internal cranial base is preferable to previous methods because the influence of brain size and shape is minimized. Although only one landmark of the upper face was utilized in this study, we feel that this is an important step toward better characterization of the craniofacial relationship.

Further work on the influence of prenatal and early postnatal brain growth on the facial growth pattern is needed to interpret species differences in facial positioning. In addition, growth of the entire facial skeleton relative to the internal cranial base should be better characterized.

Variation in upper facial positioning among fossil hominid crania reflects species differences in the relative size of endocranial and facial dimensions. We suggest that frontal lobe expansion increased total facial projection in *Homo erectus* and archaic *Homo sapiens* crania and may have limited superior facial growth. Expansion of the masticatory apparatus may relate to upper facial positioning in robust australopithecine crania. However, further research in this area is needed to clarify the effects of masticatory expansion on the facial growth pattern. Assessments of facial position in fossils should be made relative to the internal and external cranial base to evaluate the relative importance of neural and nonneural soft tissue influences on the position of the upper face.

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